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Plant defense mechanisms in insect and mite pest management: A review

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Abstract

Plants and insects have been living together for more than 350 million years. In co- evolution, both have evolved strategies to avoid each other's defense systems. This evolutionary arms race between plants and insects has resulted in the development of an elegant defense system in plants that has the ability to recognize the non-self-molecules or signals from damaged cells, much like the animals, and activates the plant immune response against the herbivores. Resistance can be categorized into non-preference (antixenosis), antibiosis, and tolerance, each stemming from specific plant characteristics. Morphological defenses such as trichomes, cuticle structure, and silica content provide mechanical barriers or disrupt herbivore feeding. Biochemical defenses include secondary metabolites like terpenes and phenolics that deter feeding and impair herbivore growth through anti-nutritional effects. Specific proteins such as proteinase inhibitors and chitinases further compromise insect digestion and development. Additionally, plant responses to herbivore attacks involve resource reallocation and nutritional adjustments that can deter herbivore colonization. For instance, resistant plant varieties may exhibit lower nutrient availability, leading to decreased herbivore fitness. By understanding these mechanisms, pest management strategies can be developed that utilize resistant genotypes to minimize the impact of herbivorous arthropods on agricultural yield and quality. This holistic approach integrates both morphological and biochemical traits to enhance plant defense, thereby fostering sustainable agricultural practices.

Keywords: Host plant resistance, morphological, biochemical, plant defense, integrated pest management

Introduction

The interactions of herbivorous arthropods with their plant hosts are complex and multifaceted [1], even when they take place in the simplified ecosystems characteristic of agriculture. The overall process by which an herbivore makes use of a plant usually involves a number of phases: a searching phase in which the herbivore moves, often in response to visual and odour cues, from a location lacking a host-plant to a potential host; a contact evaluation phase mediated by an expanded set of visual, physical, and chemical cues from the plant; and a host utilization phase in which the performance of the herbivore is influenced by interacting suites of nutrients, toxins, digestibility reducers and other factors in the plant [2-3]. Plant resistance results from the expression by the plant of resistance-related plant traits that affect one or more aspects of the herbivore's interaction with the host plant and with other plant-associated organisms. Plant resistance may be defined as the 'sum of the genetically inherited qualities' that determine the ultimate degree of damage (yield loss) done to the plant by the herbivore [4]. Plants deploy a wide array of defensive strategies that operate at multiple levels: morphological barriers, such as trichomes and cuticles; biochemical deterrents, including alkaloids and phenolics; molecular signaling through phytohormones and defense proteins; and ecological mechanisms, such as herbivore-induced plant volatiles (HIPVs), which recruit natural enemies [5].

There is a sense in which plant resistance is always an element of a pest management programme. After all, it is the interaction between the pest herbivore and the crop host, in all its complexity, that the pest manager seeks to manipulate in order to minimize the impact of the pest on crop yield and quality. By influencing the expression of resistance-related traits, the genotype of the crop is the strongest influence on this crop–pest interaction. Crop genotype is thus the foundation on which management strategies are built. In the context of pest management, however, 'plant resistance' typically references the integrated management tactic in which a resistant plant genotype is intentionally employed, alone or in combination with other tactics, to reduce the impact of herbivorous arthropods on crop yield or quality.

How plant recognizes insect herbivore

Plants recognize cues in the insect's oral secretion/saliva and in the ovipositional fluid [6-9]. Insect oral secretions contain specific elicitors such as fatty acid conjugates (FACs), which stimulate plant defense. The first plant defense elicitor identified from the oral secretions of beet armyworm, *Spodoptera exigua*, was volicitin (N-(17-hydroxylinolenoyl)-L-glutamine), whose application on maize wounds resulted in the emission of a blend of volatiles that attracted natural enemies of the pest [10]. N-linolenoyl-glu, a potential elicitor of volatiles in tobacco plants isolated from tobacco hornworm, *Manduca sexta* regurgitate [11], when applied to the wounded leaves of tobacco activates mitogen-activated protein kinase (MAPK), wound-induced protein kinase (WIPK), SA-induced protein kinase (SIPK), JA, SA, ethylene (ET) and JA-isoleucine conjugate (JA-Ile) [12]. The MAPK pathway is involved in plant growth and development and activates various signaling pathways in the host plant in response to biotic and abiotic stresses such as cold, drought, pathogens and insect attack [8]. Further, 7-epi-JA induced by FACs elicits plant defensive genes against herbivory [11]. Inceptins and caeliferins in the oral secretions of many insects also activate plant defensive pathways against insect pests [6, 7]. Plastidic ATP synthase, γ-subunit gives rise to inceptins, whereas the caeliferins are sulfated fattyacids [6, 7]. The glucose oxidase (GOX) in the saliva of *Ostrinia nubilalis* and *Helicoverpa zea* mediates the defensive signaling pathways in tomato [13, 14]. Further, salivary components of *O. nubilalis* induce the expression of Proteinase Inhibitor 2 (PIN2) and maize protease inhibitor genes in tomato and maize, respectively [14]. Some reports show the suppression of plant defensive responses by insect oral secretions. For example, oral secretions of the African cotton leafworm, *Spodopteralittoralis* and cabbage butterfly, *Pieris brassicae* cause suppression of plant defense responses in Arabidopsis resulting in increased larval weights [15].

Mechanism of plant resistance

Resistance or susceptibility of plants to insects involves a cause-and-effect relationship between the insect's response(s) to the plant and, in tum, the plants' reaction(s) to the insect; for example, lack of attraction of insects to a particular' plant for oviposition or feeding and the unsuitability of plants for insects.

Painter classified varietal resistance into 3 categories

- **Non-preference or Antixenosis:** When a plant possesses characteristics that make it unattractive to insect-pests for oviposition, feeding or shelter.
- **Antibiosis:** When the host plant adversely affects the bionomics of the insects feeding on it.
- **Tolerance:** When the damage to the host plant is only marginal despite it supporting an insect population of a size sufficient to damage severely susceptible hosts.

Causes or Bases of resistance

The non-preference, antibiosis and tolerance mechanisms of resistance result from a series of interactions between insects and plants. A number of plant characteristics are known to render the cultivars less suitable or unsuitable for feeding, oviposition and development of insects. These interactions are governed by the plant characters *viz.* morphological (biophysical) and biochemical.

Morphological adaptations or factors as a base of resistance in plants.

- Morphological defense typically refers to defense mechanisms which is related to physical structure. They range from tissue hardness, visual factors, Fregobact, Plant cuticle, Silica content to complex glandular trichomes.

1. Trichomes

The plant is often covered with epidermal outgrowths called trichomes. Trichome density negatively affects the insect feeding, ovipositional responses and the larval nutrition of insect pests in many species of plants. They originate from epidermal tissue and then develop and differentiate to produce hair-like structures. Dicotyledons are generally hairier than monocots, but trichomes can be induced in glaborous species.

Jefree classified trichomes as

- Simple unicellular
- Multicellular uniseriate
- Multicellular multiseriate
- 2-5 branched
- Stellate
- Dendritic or arboriform
- Peltate

Trichomes can act as an insect resistance mechanism in 3 ways

- As a physical barrier limiting insects' contact with the plant
- By producing toxic compounds which poison the insect through contact, ingestion or inhalation
- By producing gummy, sticky or polymerizing chemical exudates which impedes the insect

Mechanism

Dense trichomes affect the herbivory mechanically, and interfere with the movement of insects and other arthropods on the plant surface, thereby reducing their access to leaf epidermis. These can be straight, spiral, hooked, branched or unbranched and can be glandular or nongranular. Glandular trichomes secrete secondary metabolites including flavonoids, terpenoids, and alkaloids that can be poisonous, repellent, or trap insects and other organisms, thus forming a combination of structural and chemical defense [16, 17].

Example

Cotton leafhopper, *Amrasca devastans* (Dist.) on bhendi and green peach aphid, *Myzus persicae* on Solanum species. Mechanical effects depend on density, erectness, length and shape of trichomes [17].

2. Plant cuticle

Plant cuticle consist of wax, pectin & cellulose are the major components of a plant cuticle and play an important role in protecting aerial organs from damage caused by biotic and abiotic stresses. Plant waxes have the primary function of maintaining the water balance but they also interfere with insect-plant relationship either positively or negatively. They affect feeding behaviour of insects particularly settling of probing insects, acting as feeding deterrent. They also affect colonization and oviposition [18].

Mechanism

Epicuticular waxes are the major components of a plant cuticle and play an important role in protecting aerial organs from damage caused by biotic and abiotic stresses. The slipperiness on plant surface is increased due to waxes, which reduces the grip of insect herbivores and prevent them from feeding or ovipositing on the leaf surfaces.

Example

In castor, no bloom and single bloom varieties have a relatively low population of the castor semilooper, *Achaea janata* L. compared to varieties with double and triple blooms. So also, the resistance to the leafhopper, *Empoasca jlavescens* (F.) has been found to be associated with the waxy blooming. The resistance to the mite, *Tetranychustelarius* Koch in castor has also been associated with the leaf bloom. Young leaves of *Eucalyptus globulus* possess wax layer on its surface making it slippery and reduces adherence herbivorous psyllids [19].

3. Silica content

Its increased levels affect the mandibles of the insects and greatly reduce feeding. Its presence and distribution in leaves also play an important role. In addition to acting as a mechanical barrier, Si can reduce pest damage by enhancing the induced chemical defenses of plants following insect attack. Silicon acts as an abiotic elicitor of systemic stress signals, mediated by phytohormone pathways, leading to the efficient synthesis of defensive compounds [20].

Mechanism

Deposition of Si increases the thickness of the wall and the size of the vascular bundle. Protection, storage, support and strengthening leads to the increased irreversible wear of mouthparts when insects are feeding, therefore deterring chewing insects. Its increased levels affect the mandibles of the insects and greatly reduce feeding. Its presence and istribution in leaves also play an important role [21].

Example

High-silica grasses rye grass (*Lolium perenne*) affect feeding preferences and digestion efficiency of insects showing that silica levels correlated with increased mechanical protection [22]. Silica in rice leaves against stem borer. The use of plant resistance inducers is considered an environmentally friendly strategy to efficiently decrease insect pest populations. In addition to acting as a mechanical barrier, Si can reduce pest damage by enhancing the induced chemical defences of plants following insect attack. Silicon acts as an abiotic elicitor of systemic stress signals, mediated by phytohormone pathways, leading to the efficient synthesis of defensive compounds [23].

Toughness and thickness of cell wall of tissue of leaf’s

Tough and thick plant tissue cause mechanical obstruction to feeding and oviposition of insect pests Leaf toughness interferes with the penetration of plant tissues by mouthparts of piercing & sucking insects and increase mandibular wear in biting-chewing herbivores. The cell walls of leaves are also reinforced during feeding through the use of different macromolecules, such as lignin, cellulose, suberin and callose, together with small organic molecules, such as phenolics, and even inorganic silica particles [24].

Example

The thickness of leaf midrib in sugarcane recorded significant and negative correlation with incidence of top borer *Scirpophaga excerptalis* [25]. Roots eaten by insect herbivores exhibit extensive regrowth, both in density, as seen in Trifolium repens eaten by *Sitona lepidus* (clover root weevil), and in quantity, as observed in *Medicago sativa* (alfalfa) attacked by clover weevil (*Sitona hispidulus*).

4. Visual factors

Plant colour contributes to non-preference in some cases. For example, red cabbage and red leaved Brussel’s sprouts are less favored than green types by butter flies and other Lepidoptera for oviposition. In cotton, red plants are less preferred than green by bollworms. Yellow colour is preferred by aphids. Green and blue green is preferred by cabbage butterfly. Dark green preferred by rice leaf folder.

5. Other Characters

Many other plant characters contribute to insect resistance.

a. In tree cotton, varieties with narrow lobes and leathery leaves are more tolerant to jassids than those with broad lobes and succulent leaves.
b. Cotton varieties with long pedicel are more resistant to bollworms than those with short pedicel. Long pedicel makes the movement of bollworm difficult from one boll to another.
c. Nectariless cotton varieties are devoid of nectar glands. Insect visit on such varieties is lesser than those which posse’s nectar glands. Insect visit on such varieties is lesser than those which possess nectar glands.
d. Frego bract is a mutant type of floral bract in upland cotton. It is an important insect resistant trait; however, some reports in the literature show that frego bract gene has some negative effects on growth and fiber quality of cotton. They help reduce the number of eggs laid and subsequent damage by boll weevils *Anthonomous grandis. Cotton* genotypes with frego bract do not provide shelter for the bollworms to lay eggs. Moreover, such types are suitable for better coverage of insecticidal sprays.
e. Plants can offer predators like ants, mites and bugs small chambers in the juncture of the midrib and the vein used as nesting or refuge sites. Ant nesting sites are restricted to the tropics, while mite and bug leaf nesting sites can also be found in temperate regions [26].
f. Extrafloral nectar (EFN) is secreted on leaves and shoots by plants and helps to attract predators and parasitoids. EFN is evolutionary and more ancient than floral nectar, secreted by more than 70 species of angiosperm, gymnosperms and ferns [27].
g. Hypersensitivity of plant tissues. Larvae of the melon leaf miner, *Liriomyza pictella*, mining in young leaves of snap dragon plants are crushed by the rapidly proliferating wound tissue, and in eggplant, the tissue surrounding the larvae dries up, thus stopping their development

Biochemical base of resistance in plants

Plant produced chemical compounds have mainly divided into primary and secondary metabolids. Apart from the primary metabolites used for growth, development and reproduction, plants also synthesize a broad range of secondary metabolites, also known as bioactive specialized compounds, which are toxic to herbivores and act as defense compounds [28]. These are targeted especially against biological systems unique to herbivores, such as the nervous, digestive and endocrine organs, and are produced both constitutively and upon induction. Plant secondary metabolites can be divided chemically in distinct groups *viz*: terpenes, phenolics [29].

1. **Terpenes:** These compounds are biosynthesized from acetyl-CoA or glycolytic intermediates [30]. On the basis of C_5 units, we can classify the terpenoids as C_5 (hemiterpenes), C_{10} (monoterpenes), C_{15} (sesquiterpenes), C_{20} (diterpenes), C_{25} (sesterpenes), C_{30} (triterpenes), C_{40} (tetraterpenes), $>C_{40}$ (polyterpenes) [31]. The insecticidal activity of the terpenes is either due to their action as antifeedants, toxins or as modifiers of insect development. Some important terpenoid deterrents and toxins are gossypol, polygodial, glaucolide-A, pyrethroids and cucurbitacin. Desert plants consist of a number of terpenoids and sesquiterpenoids that are found to be good insect deterrents. Azadirechtin (triterpene) is one of the most potent feeding deterrents to many insects, exerts various toxic effects and inhibits egg maturation**.**

2. **Phenolics:** Phenolic are aromatic ring bearing compounds with one (phenol) or more (polyphenol) hydroxyl substituents which include nearly 10,000 individual compounds derived from the shikimic acid and malonic acid pathways taking place in the above ground tissues [32]. These compounds help in defense by repelling feeding herbivores and inhibiting enzymes, by absorbing harmful ultraviolet radiation, as mechanical support in the plant, and by reducing the growth of nearby competing plants. Some important phenolic defense compounds are coumarin, furano-coumarins, ligin, flavonoids, isoflavonoids and tannins. Isoflavonoids isolated from wild relatives of chickpea, *Cicer arietinum,* deter larval feeding by *Helicocoverpa armigera*. Salicylates in Salix leaves reduces feeding and growth of polyphagous larvae of *Operophtera brumata* [33].

3. **Anti nutritional/ digestive proteins:** Plants can also defend themselves by producing proteins that reduce the nutrient value to the attacking insect or causes physical damage to the insect digestive tract. The major classes of such defense proteins are:

- α-amylase inhibitor.
- Chitinase.
- Lectin.
- Polyphenol Oxidases.
- Proteinase inhibitor.

a. **α-amylase inhibitor:** These inhibit α-amylase, enzyme that plays a role in digestion of starch and glycogen in insects [34] The activities of these inhibitors are directed against α-amylases from insects and microorganisms [35], used for starch breakdown, and seldom affect the plant amylases α-amylase inhibitor from cowpea seeds, *Vignaunguiculata*, inhibited α-amylase from *Callosobruchus maculates* larvae by 50%. Triticale-α amylase inhibitor has a strong inhibitory activity on *Eurygaster integriceps* gut α-amylase [36].

b. **Chitinase**: Chitin is the major component of the insect cuticle and peritrophic membrane and chitinases is used as a pest management tool to degrade peritrophic membrane of insect alimentary canal [37]. Development of Colorado potato beetle is inhibited by poplar chitinase in transgenic tomato [38], transgenic *N. tabacum* repels *M. sexta* [39], and *Lacanobia oleracea* (tomato moth) is repelled by transgenic *S. tuberosum* [40].

c. **Lectin:** One particular class of entomotoxic proteins present in many plant species is the group of carbohydrate binding sugar-proteins or lectins found especially in storage organs [41]. Lectins come into contact with the glycoproteins lining the intestinal area of insect inhibiting the absorption of nutrients. First lectin to which ant insect properties were ascribed on the basis of its deleterious effect on the larvae of bruchid beetle *Callosobruchus maculatus* [42], *Zabrotessubfasciatus* (bean weevil) are found in *P. vulgaris* [43].

d. **Polyphenol Oxidases:** Polyphenol oxidases (PPOs) are ubiquitous copper-containing anti-nutritive enzymes which use molecular oxygen to oxidize common orthodiphenol compounds to highly reactive quinines cause the typical browning of damaged tissues. PPO generated quinones further react with amino acids reducing their availability. It causes typical browning of plant extracts and damaged plant tissues. Overexpression of PPO genes in tomato and hybrid aspen (*Populustremula* × *Populus alba*) resulted in increased insect resistance, and silencing of PPOs resulted in increased susceptibility to insect herbivory [44].

e. **Proteinase inhibitors:** Proteinase inhibitor act as antimetabolic proteins, which interfere with the digestive process of insects. These inhibit proteases present in insect guts, causing a reduction in the availability of amino acids necessary for their growth and development. Pepstatin, a powerful and strong inhibitor of aspartyl proteases has been shown to inhibit proteolysis of the midgut enzymes of Colorado potato beetle, *Leptinotarsa decemlineata* [45].

Reallocation of Resources: Plant responses to herbivore attacks are influenced by their vascular structure and phyllotaxy, which govern the movement of signals and resources between different plant parts. This architectural constraint plays a crucial role in determining the plant's defensive capabilities. For example, signaling molecules may travel via direct vascular connections to cue the systemic induction of proteinase inhibitors and related genes in orthostichous leaves of poplar, tomato, and tobacco [46-48]. To protect valuable resources, they might be reallocated by the plant upon attack. For instance, *Centaureamaculosa* (spotted knapweed) allocates more nitrogen to the shoots upon attack by *Agapetazoegana* (sulphur knapweed moth) [49]. Reallocation can also be directed from shoot to root. Also, reallocation of starch from *Populus tremuloides* (quaking aspen) leaves to roots was caused by exogenously applying JA to the leaves [50].

Conclusions

Plant resistance to insect herbivores is a sophisticated and multifaceted defense system that has evolved through the ongoing evolutionary arms race between plants and insects. This complex interplay involves a range of physical and biochemical mechanisms that allow plants to recognize, respond to, and protect themselves against insect attacks. Plants can detect specific insect elicitors in oral secretions and oviposition fluids, triggering cascades of defensive responses. These responses manifest as antixenosis (non-preference), antibiosis, and tolerance mechanisms, encompassing both physical barriers and biochemical warfare. Morphological adaptations such as trichomes, waxy cuticles, silica content, and tissue toughness create formidable obstacles to insect feeding and oviposition. Simultaneously, plants deploy an arsenal of biochemical defenses, including secondary metabolites like terpenes and phenolics, as well as anti-nutritional proteins that deter or harm insect herbivores. Plants can also strategically reallocate resources in response to herbivory, protecting valuable assets from damage. The effectiveness of these defense mechanisms varies based on plant species, insect species, and environmental conditions, highlighting the dynamic nature of plant-insect interactions. Understanding these intricate resistance mechanisms is crucial for developing pest-resistant crop varieties and implementing sustainable pest management strategies in agriculture, ultimately contributing to improved crop protection and food security in the face of evolving insect threats.

Author contributions

SS, SC, RKD and JSV conceptualized and developed the studyframework. SSandSCprepared the preliminary draft of the manuscriptwith inputs from RKD and JSVand contributed to editing and refining different manuscript sections. All authors reviewed and approved the submitted version.

References

1. Rasmann S, Agrawal AA. Plant defense against herbivory: progress in identifying synergism, redundancy and antagonism between resistance. Current Opinion in Plant Biology,2009:12:1–6.
2. Bhardwaj SP, Sharma S, Bhardwaj S. Effect of host plant nutrition on development and population build up of European red mite, *Panonychus ulmi* (Koch) on apple. Acta Horticulture,2005:696(2):399–405.
3. Sharma S, Bhardwaj SP, Bhardwaj S. Effect of nitrogen, phosphorus and potash on population dynamics of European red mite, *Panonychus ulmi* (Koch) on apple. Indian Journal of Entomology,2005:72(1):60–65.
4. Smith CM, Clement SL. Molecular bases of plant resistance to arthropods. Annual Review of Entomology,2012:57:309–328.
5. Shashikala B, Divya DM, Benakashree C, Gaurav VRS, Shukla A, Sachin RK, *et al*. Plant defense mechanisms against insect herbivores: integrating biochemical, molecular, and ecological perspectives. Journal of Advances in Biology & Biotechnology,2025:28(9):730–742. https://doi.org/10.9734/jabb/2025/v28i92921
6. Schmelz EA, Carroll MJ, LeClere S, Phipps SM, Meredith J, Chourey PS, *et al*. Fragments of ATP synthase mediate plant perception of insect attack. Proceedings of the National Academy of Sciences of the United States of America,2006:103:8894–8899.
7. Alborn HT, Hansen TV, Jones TH, Bennett DC, Tumlinson JH, Schmelz EA, *et al*. Disulfooxy fatty acids from the American bird grasshopper *Schistocerca americana*, elicitors of plant volatiles. Proceedings of the National Academy of Sciences of the United States of America,2007:104:12976–12981.
8. Wu J, Hettenhausen C, Meldau S, Baldwin IT. Herbivory rapidly activates MAPK signaling in attacked and unattacked leaf regions but not between leaves of *Nicotiana attenuata*. The Plant Cell,2007:19:1096–1122.
9. Howe GA, Jander G. Plant immunity to insect herbivores. Annual Review of Plant Biology,2008:59:41–66.
10. Alborn T, Turlings TCJ, Jones TH, Stenhagen G, Loughrin JH, Tumlinson JH, *et al*. An elicitor of plant volatiles from beet armyworm oral secretion. Science,1997:276:945–949.
11. Halitschke R, Schittko U, Pohnert G, Boland W, Baldwin IT. Molecular interactions between the specialist herbivore *Manduca sexta* and its natural host *Nicotiana attenuata*. Plant Physiology,2001:125:711–717.
12. Navya E, Vitty BS, Kumari JA, Supraja KVL, Raj DP, Venkatesh P. Ecological warfare: natural plant defense mechanism against insect pests. Journal of Experimental Agriculture International,2025:47(4):139–150. https://doi.org/10.9734/jeai/2025/v47i43364
13. Tian D, Peiffer M, Shoemaker E, Tooker J, Haubruge E, Francis F, *et al*. Salivary glucose oxidase from caterpillars mediates the induction of rapid and delayed-induced defenses in the tomato plant. PLOS One,2012:7:e36168.
14. Louis J, Peiffer M, Ray S, Luthe DS, Felton GW. Host-specific salivary elicitor(s) of European corn borer induce defenses in tomato and maize. New Phytologist,2013:199:66–73.
15. Consales F, Schweizer F, Erb M, Gouhier-Darimont C, Bodenhausen N, Bruessow F, *et al*. Insect oral secretions suppress wound-induced responses in *Arabidopsis*. Journal of Experimental Botany,2012:63:727–737.
16. Thakur M, Mahajan R, Sharma S, Mehta PK. Bioefficacy of *Podophyllum hexandrum* and podophyllotoxin against cruciferous pests. Indian Journal of Plant Protection,2007:35(1):43–46.
17. War AR, Paulraj MG, Ahmad T, Buhroo AA, Hussain B, Ignacimuthu S, *et al*. Mechanisms of plant defense against insect herbivores. Plant Signaling and Behavior,2012:7(10):1306–1320.
18. Khan ZR, Ward JT, Norris DM. Role of trichomes in soybean resistance to cabbage looper. Entomologia Experimentalis et Applicata,1986:42(2):109–117.
19. Sharma S, Bhardwaj SP, Thakur M. Morphology and life cycle of the apple leafroller, *Archips termias* Meyrick, infesting apple in Himachal Pradesh. Indian Journal of Entomology,2005:67(4):289–290.
20. Walters D. Plant defense: warding off attack by pathogens, herbivores and parasitic plants. Wiley Blackwell, 2011, 30–31.
21. De Vos M, Van Oosten VR, Van Poecke RMP, Van Pelt JA, Pozo MJ. Signal signature and transcriptome changes of *Arabidopsis* during pathogen and insect attack. Molecular Plant Microbe Interactions,2005:18:923–937.
22. Santos MC, Junqueira AMR, Sá VGM, Zanuncio JC, Serrão JE. Efeito do silício em aspectos comportamentais e na história de vida de *Tuta absoluta*. Brasil Agropec,2012:2:76–88.
23. Massey FP, Ennos AR, Hartley SE. Silica in grasses as a defence against insect herbivores. Journal of Animal Ecology,2006:75(2):595–603.
24. Fauteux F, Rémus-Borel W, Menzies JG, Bélanger RR. Silicon and plant disease resistance against pathogenic fungi. FEMS Microbiology Letters,2005:249:1–6.
25. Sushil SN, Chandra A, Roy S, Jaiswal AK, Singh MR, Pathak AD. Determination of morphological and biochemical basis of resistance against top borer, *Scirpophaga excerptalis*. Sugar Tech,2020:22:259–265. https://doi.org/10.1007/s12355-019-00767-0
26. Romero GQ, Benson WW. Biotic interactions of mites, plants and leaf domatia. Current Opinion in Plant Biology,2005:8:436–440.
27. González-Teuber M, Heil M. Nectar chemistry is tailored for both attraction of mutualists and protection

from exploiters. Plant Signaling and Behavior,2009:4:809–813.

28. Wittstock U, Gershenzon J. Constitutive plant toxins and their role in defense against herbivores and pathogens. Current Opinion in Plant Biology,2002:5(4):300–307.
29. Khan MM, Mohammad TA. Role of secondary metabolites in defense mechanisms of plants. Biology and Medicine,2011:3(2):232–249.
30. Engelberth J. Secondary metabolites and plant defense. Plant Physiology, 2006, 315–344.
31. Singh B, Sharma RA. Plant terpenes: defense responses, phylogenetic analysis, regulation and applications. Biotechnology,2015:5(2):129–151.
32. Nuessly GS, Scully BT, Hentz MG, Beiriger R, Snook ME, Widstrom NW. Resistance to *Spodoptera frugiperda* and *Euxesta stigmatias* in sweet corn. Journal of Economic Entomology,2007:100:1887–1895.
33. Lattanzio V, Lattanzio VMT, Cardinali A. Role of phenolics in resistance mechanisms of plants against fungal pathogens and insects. Phytochemical Advances Science Research,2006:23:67.
34. Sales PM, Souza PM, Simeoni LA, Silveira D. α-Amylase inhibitors: a review of raw material and isolated compounds from plant source. Journal of Pharmaceutical Sciences,2012:15(1):141–830.
35. Franco OL, Rigden DJ, Melo FR, Grossi-de-Sa MF. Plant α-amylase inhibitors and their interaction with insect α-amylases. European Journal of Biochemistry,2002:269(2):397–412.
36. Mehrabadi M, Bandani AR, Saadati F. Inhibition of Sunn pest, *Eurygaster integriceps*, α-amylases by α-amylase inhibitors from triticale. Journal of Insect Science,2010:10:179.
37. Chandrasekaran R, Revathi K, Thanigaivel A, Kirubakaran SA, Senthil-Nathan S. *Bacillus subtilis* chitinase has insecticidal activity against *Spodoptera litura*. Pesticide Biochemistry and Physiology,2014:116:1–12.
38. Sharma N, Sharma KP, Gaur RK, Gupta VK. Role of chitinase in plant defense. Asian Journal of Biochemistry,2011:6(1):29–37.
39. Ding X, Gopalakrishnan B, Johnson LB, White FF, Wang X, Morgan TD, *et al*. Insect resistance of transgenic tobacco expressing an insect chitinase gene. Transgenic Research,1998:7:77–84.
40. Gatehouse AMR, Davison GM, Newell CA, Merryweather A, Hamilton WDO, Burgess EPJ, *et al*. Transgenic potato plants with enhanced resistance to the tomato moth *Lacanobia oleracea*. Molecular Breeding,1997:3:49–63.
41. Vandenborre G, Smagghe G, Van Damme EJM. Plant lectins as defense proteins against phytophagous insects. Phytochemistry,2011:72:1538–1550.
42. Peumans WJ, Van Damme JMV. Lectins as plant defense proteins. Plant Physiology,1995:109:347–352.
43. Osborn T, Alexander D, Sun S, Cardona C, Bliss F. Insecticidal activity and lectin homology of arcelin seed protein. Science,1998:240:207–210.
44. Araji S, Grammer TA, Gertzen R, Anderson SD, Mikulic-Petkovsek M, Veberic R. Novel roles for polyphenol oxidase in secondary metabolism and regulation of cell death in walnut. Plant Physiology,2014:164(3):1191–1203.
45. Habib H, Fazili KM. Plant protease inhibitors: a defense strategy in plants. Biotechnology and Molecular Biology Review,2007:2(3):68–85.
46. Shulaev V, Leon J, Raskin I. Is salicylic acid a translocated signal of systemic acquired resistance in tobacco. Plant Cell,1995:7:1691–1701.
47. Orians CM, Pomerleau J, Ricco R. Vascular architecture generates fine scale variation in systemic induction of proteinase inhibitors in tomato. Journal of Chemical Ecology,2000:26:471–485.
48. Schittko U, Baldwin IT. Constraints to herbivore-induced systemic responses in *Nicotiana attenuata*. Journal of Chemical Ecology,2003:29:763–770.
49. Newingham BA, Callaway RM, Bassirirad H. Allocating nitrogen away from an herbivore. Oecologia,2007:153:913–920.
50. Babst BA, Ferrieri RA, Gray DW, Lerdau M, Schlyer DJ, Schueller M, *et al*. Jasmonic acid induces rapid changes in carbon transport and partitioning in *Populus*. New Phytologist,2005:167:63–72.